

# Evolutionarily stable germination strategies with time-correlated yield

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## Abstract

We investigate the effect of auto-correlated yield on the evolutionarily stable germination fraction of dormant seeds. By using both analytics and numerics, we first show that in a regime of small fluctuations a positive correlation reduces dormancy and a negative correlation enhances dormancy. By extending the numerical analysis we also show that in the regime of large fluctuations a more complex picture emerges where also negative correlations can reduce dormancy.

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## 1. Introduction

Plant species living in deserts and strongly varying environments need to keep a permanent soil seed bank in order to avoid extinction (Cohen, 1966, 1967; Venable and Lawlor, 1980; Bulmer, 1984; Ellner, 1985a, b; Brown and Venable, 1986; Venable and Brown, 1988; Gutterman, 2002; Rees, 1994). This is achieved by means of delayed germination, which is a mechanism that allows seeds to remain dormant in the soil even if optimal conditions for germination are met.

In this work, we describe delayed germination as an evolutionary strategy in stochastic environments (Cohen, 1966; Bulmer, 1984; Ellner, 1985a, b). According to this approach, it is the large level of the environmental variation entering through the between year changes of the yield  $Y$ , which is the average number of seeds per plant, that determines the degree of dormancy of the seeds.

In order to simplify the formulation of models, it is usually assumed that all seeds produced after one given season share the same germination probability  $g$  so that, for large seed banks,  $g$  is the fraction of germinating seeds.

The first study dedicated to the determination of the germination fraction as an evolutionary strategy was presented by Cohen (1966). There, the germination fraction

was obtained as optimal strategy in a stochastic environment. The assumption of that work was that the dynamics of the seed bank is described by a multiplicative process without density dependence. Due to this assumption, it was possible to identify the optimal strategy as the value of the germination fraction that maximized the geometric average of the growth rate. Under the simple assumption that only two kinds of season occurs, namely good season with probability  $p$  and a season with no seed production with probability  $1 - p$ , Cohen (1966) showed that the optimal germination fraction is approximately equal to  $p$ . This study showed that under certain simplifying assumptions, there is a simple relationship between the optimal  $g$  and the statistical properties of the environment. This strategy was called bet-hedging (Cohen, 1966; Slatkin, 1974; Philippi and Seger, 1989).

A further major step in the development of the theory was presented by Bulmer (1984) and Ellner (1985a, b), where density dependence effects have been included in the dynamics of the seed bank. The density dependence was introduced in terms of a decreasing seed production as function of the seedlings density. In these cases, the number of seeds in the seed bank fluctuates around a certain average. The nature of these fluctuations depended on the statistical properties of the environmental fluctuations. Since there was no long-term growth of the size of the seed bank, it was not possible to apply the method used by Cohen (1966) to compute the optimal germination strategy.

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In fact, what had to be done was to study this system by means of the invasibility analysis in order to find the evolutionarily stable strategy (Maynard Smith, 1982) for the system. It was then possible to show that large fluctuations of the environmental variables and of the seed bank size select for small evolutionarily stable germination fractions.

Recently, Valleriani (2005) has also shown that the evolutionarily stable value of  $g$  depends on the moments of the distribution of the yield in a rather non-trivial way. In particular, it was shown that the second, third and fourth moment act differently in the determination of the evolutionarily stable germination fraction.

Of interest here is another property of environmental stochasticity, namely the auto-correlation of its variables. It was stressed already some time ago (Halley, 1996) that environmental noise might be correlated in time and that the correlations should have an effect on the population dynamics, on the risk of extinction, and on community composition (Lawton, 1988; Steel and Henderson, 1984; Ripa et al., 1998; Halley and Kunin, 1999). Recently, Levine and Rees (2004) have shown that the auto-correlation properties of the year quality can influence the survival of rare annuals in a grass-dominated system. Their conclusion was that positive auto-correlation would not enhance coexistence whereas negative correlations would do. The basic mechanism was that positive year-to-year correlations in the stochastic variable would tend to produce long series of seasons with the same quality and favor the grasses. On the other hand, negative correlations would tend to produce short series and a strong year-to-year variability.

Another study by Vasseur and Yodzis (2004) showed moreover that most, if not all environmental variables (e.g. precipitation, temperature) are auto-correlated, with properties of the correlation depending on the particular environment. Although Vasseur and Yodzis (2004) did not propose any particular general model on how to take into account their observation, they correctly stressed that the presence or absence of effects due to correlated noise must be taken into account in ecological modeling. In particular, Vasseur and Yodzis (2004) found that going from the inland towards the sea we have to expect an increase in the length of the auto-correlation. Thus, if we want to compare populations located at different geographical positions it is necessary and convenient to have a theory that is able to incorporate this important aspect of the environmental variables.

The model system we want to consider here is given by annual plants in strongly stochastic and unpredictable environment like deserts. The most natural stochastic variable that enters those models is given by average yearly precipitation because this, at the end, influences the yield of the plants. Although we do not have a strong argument to say that average yearly precipitation must be auto-correlated, the work of Vasseur and Yodzis (2004) tells us that it is likely that it will be so.

We consider here the seed bank dynamics governed by the equation

$$S(t+1) = S(t)[gf(gS(t))Y(t) + (1-g)(1-d)], \quad (1)$$

where  $S(t)$  is the size of the soil seed bank at the beginning of season  $t$ . The stochastic variable  $Y(t)$  is the average yield per adult plant in season  $t$ . The distribution of  $Y$  is given by the between year variation of the average yield per adult plant and in this and the next section we assume that it is a continuous variable. As we shall see later, in the numerical part of this work we will consider a discrete  $Y$ . The variable  $g$  in Eq. (1) is the fraction of  $S(t)$  that germinates and  $d$  is the fraction of non-germinating seeds, given by  $(1-g)S(t)$ , that become unviable during season  $t$ . The function  $f(s)$  is responsible for density dependence and gives the fraction of germinating seeds  $s = gS(t)$  that survive competition. We will assume (Ellner, 1985b; Nilsson et al., 1994; Mathias and Kisdi, 2002) that this function is given by the reciprocal yield model

$$f(s) = \frac{K}{K+s}, \quad (2)$$

where  $K$  is the carrying capacity of the system, namely the maximum density of adult plants supported by the environment.

The previous studies on evolutionarily stable germination fraction assumed that the stochastic variable  $Y(t)$  is not correlated. In this work instead we consider a correlated function as follows. Let us define  $y(t) = Y(t) - \bar{Y}$ , where  $\bar{Y}$  is the average value of  $Y$ . We will then define

$$M_2(n) = \langle y(t)y(t+n) \rangle, \quad (3)$$

the two-point correlation function of  $y(t)$ , where  $M_2(0)$  is the variance of the distribution of  $Y$ , and where  $\langle \phi \rangle$  denotes the long time average of the function  $\phi$ . In the following, we will sometimes also use the short form  $\bar{\phi}$  to denote this time average.

We would then recover the function for non-correlated yield when for  $n > 0$  we have  $M_2(n) = 0$ . In principle,  $M_2(n)$  can be positive or negative depending on whether the two values of  $y$  are positively or negatively correlated.

The determination of the evolutionarily stable value of  $g$  occurs by exploiting the method of invasibility analysis (Bulmer, 1994). This method, already extensively discussed in the literature (Bulmer, 1984; Ellner, 1985a, b) provides the Evolutionarily Stable Strategy (ESS), which is given as solution of the equation (Bulmer, 1984; Ellner, 1985a)

$$\left\langle \frac{f(gS(t))Y(t) - (1-d)}{gf(gS(t))Y(t) + (1-g)(1-d)} \right\rangle = 0. \quad (4)$$

To solve Eq. (4) it is necessary to numerically perform the time average over many generations of the dynamics given by Eq. (1) for many different values of  $g$  until the value that satisfies Eq. (4) is found (Bulmer, 1984; Ellner, 1985a). For this reason we will hereafter refer to the solution of Eq. (4) as the numerical solution and we will

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